SOME NOTES ON HEREDITY IN THE COCCINELLID GENUS ADALIA MULSANT.*

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It is the purpose of this paper to give a report of some experimental investigations in heredity which were made with four different forms belonging to the genus *Adalia* Mulsant. These forms shall herein be designated as *melanopleura* Leconte, *annectans* Crotch, *coloradensis* Casey, and *humeralis* Say.†

Melanopleura (Fig. A, Pl. XIX), as met with in this paper, is described as follows: Head black, with fine apical line of white, and with a whitish triangle next each eye with the apex pointing mesad and nearly reaching the median line. Sometimes a median strip of whitish connects these spots and extending forward to the apical line, which may also widen, leaves only a pair of black spots or brownish dots, one on either side of the median line on the anterior part of the head. (See head markings in Figures A, B, C, and F, Pl. XIX). Pronotum pale, with black M-shaped design and a lateral black spot, except in an unusually albinic form where the spot is absent or represented by a mere dusky area. The black spot when present may vary from a moderate sized area well enclosed by the surrounding white, to a large area which may break more or less widely through the surrounding white so as to connect with the M design. See pronotum markings in Figures A, B, and C, Pl. XIX). The basal marking is usually large in this form but may be rather small in some cases. Elytra brownish red and immaculate, or with faint dot on lateral margin of each elytron. Legs yellowish brown, darker on outer margin. Length 4–6 mm., width 3–4 mm.

Annectans, Figures B, C, and F, Plate XIX, includes quite a range of variation. The group as met with in this study is described as follows: Head as in *melanopleura*, pronotum as

* This paper is an outgrowth of breeding cage work with the *Coccinellids*, assigned me by Professor Gillette as a part of his Adams Fund project on Life Histories of the Plant Lice and Their Enemies.

† These determinations are according to Major Thos. L. Casey, who very kindly criticized my determinations of the forms referred to in this paper, excepting that *annectans* includes also an unusual and rather rare form (Fig. F, Pl. XIX), the status of which seems to me a little uncertain, but which Mr. C. W. Leng determines as *annectans*. Lacking any biological proof to the contrary I have included it under *annectans*.

given for *melanopleura* except that the basal marking is on the average somewhat smaller and is, in rare cases, even absent. The lateral black spot also is absent in an unusually albinic form, Figure F, Plate XIX. Elytra reddish yellow, usually lighter than *melanopleura*, quite yellowish for several weeks after emergence, becoming redder with age, though some never develop much of the red color. In the individuals reared of the more albinic form, Figure F, Plate XIX, the red color began to appear immediately after emergence but was paler in the region of the spots, giving a sort of blotchy appearance. This paler area may persist even in old beetles which have hibernated. Each elytron typically with a longitudinal posteriorly pointed black dash from the base at each side of the suture, and two sub-basal spots, the outer more basal, also with a transverse series of three black spots just before the middle, and two more at apical fourth, the outer very close to the margin. These black spots may vary from mere dots with some absent, to large blotches which may have more or less tendency to confluence; so that in color pattern many resembled *ovipennis* Casey, and a very few came very close to *transversalis* Casey as figured by Johnson.* Mr. Casey, however, to whom I submitted specimens of these beetles, says that they are not his species as they do not show the proper punctuation. Some specimens show a rather definite pattern of red spots, two on each elytron, one a large oblong spot at the humerus and the other a smaller round spot close to the suture and between the middle and apical series of black spots. Legs and size as in *melanopleura*.

In the more albinic form, Figure F, Plate XIX, the anterior spots were always lacking and the middle and apical series were irregularly represented. Altogether this form differs from the rest of the group in three respects; namely, in lacking the anterior or basal elytral black spots, the absence of the lateral black spots on the pronotum, and in the presence of the redder coloration of the elytra. Three individuals of this form appeared in one batch of *annectans*, and one in another batch of *annectans*, also two from a batch of larvae, from *melanopleura* parents, which produced both *melanopleura* and *annectans*. In these broods there were also some individuals which might be

* Johnson, Roswell H., 1910—Determinate Evolution in the Color Pattern of the Lady-beetles, Carnegie Institution of Washington. Pub. No. 122. Papers of the Station for Experimental Evolution, No. 15.

considered as intergrading forms to some extent. This form presents a rather strikingly different appearance from the rest of the group, since all of these characters seem as a rule to go together, making a rather pronounced gap in the series of variation. It seems indeed to be closer to *coloradensis* than to *annectans*. Furthermore, among the 109 *annectans* which were reared from eggs of two *annectans* females and two *melanopleura-annectans* hybrid females, mated with one *annectans* male and one *melanopleura* male, not one of these forms appeared, which fact seems to show that it is not a common fluctuating variation at least. It seems that the heredity might be segregate and experiments are now in progress to determine this point. It is on this account that I have thought best to call attention to it separately though for the rest of this paper it will be included under *annectans*.

Coloradensis Casey, Fig. E, Pl. XIX, is described as follows: Head black with fine apical margin of whitish, and triangular pale spot next each eye as found in *annectans*. Pronotum black with very fine apical pale margin sometimes obliterated, the posteriorly pointed median pale dash from the apical margin very small when present, sides with same pale pattern as *melanopleura* but lacking the black lateral spot, basal marking absent. Elytra brownish red, about the same color as *melanopleura*, with a duplex black spot at the middle, sometimes in the form of a band, sometimes appearing as two separate spots, also a similar series of spots, two in number at apical fourth, the inner one the larger. Legs and size as in *melanopleura*, but the shape perhaps a little more narrowly oval.

Humeralis, Say, Figure D, Plate XIX; Head same as in *melanopleura*, except that sometimes a different pattern appears as shown in Figure D, Plate XIX. Pronotum black with fine apical line and narrow side margins pale, apical line sometimes obliterated, basal marking always absent. Elytra black with a large oblong yellowish red to bright red spot at humerus and another small round one at three-fifths and close to the suture. The red marking on the elytra seems identical with the red pattern above mentioned as appearing in some specimens of *annectans*. Legs and size same as given for *melanopleura*, shape usually a little more rounded posteriorly.

The work with these forms was at first undertaken merely for the purpose of obtaining specimens for life history drawings of *melanopleura* and *annectans*. In rearing these forms the

fact of their interbreeding with each other and with *humeralis* was discovered, and then the work was directed along the line of heredity investigation. About four hundred beetles were reared to maturity from about three thousand eggs hatched. These beetles proved much more difficult to rear than the larger species such as *Hippodamia convergens* and *Coccinella quinque-notata* because of their more limited range of food and more delicate constitutions. All large aphids brought disaster in the breeding cage and sometimes even the small cottonwood louse, *Chaitophorus populicola* Thos. was rejected. In the latter case it was perhaps due to an odor left by a certain species of attendant ants, since these lice did not always prove objectionable. One feed of unfavorable lice would sometimes cause the death of from one-half to nine-tenths of a cage of larvae.

Work was begun with these beetles with the capture, May 13, 1910, in the foothills near Fort Collins, Colorado, of a pair of *annectans*. Eggs of this female were laid in the laboratory and the larvae reared. When the beetles eight in number emerged, four proved to be like the parents and four were *humeralis*. Three subsequent batches of larvae giving nine adults, were reared from eggs laid by this female and her spotted daughters with the result that three of the beetles were *annectans* and six were *humeralis*.

For the purpose of obtaining more material and also of ascertaining how frequently such mixing occurred, two or three dozen pupae of this species were collected outdoors, and as soon as the beetles emerged and the colors developed the different forms were isolated in separate cages. About fifteen percent were *humeralis* and the rest were about evenly divided between *melanopleura* and *annectans*. The humeralis beetles escaped by accident, but from the eggs of the other forms a considerable number of larvae were reared to maturity. From the eggs laid in the *melanopleura* cage thirty beetles were reared, and in each batch a large proportion were *annectans*, sometimes over half the batch and once the entire batch. Practically the same proportions were obtained from eggs of one or two females captured at other times. Besides the forms already mentioned three individuals of *coloradensis* appeared among the progeny of the above mentioned cage. Unfortunately these were not used for breeding purposes but were pinned up and put in the collection. Breeding experiments are now, however, in progress with this form.

From the cage of *annectans* only *annectans* were obtained. Twenty-five adults were reared from eggs laid in this cage, and fifty-seven from eggs laid by a female tested in a way to be explained later, making eighty two beetles in all, and every one proved to be *annectans*. The eggs of one *annectans* female captured out of doors produced several *melanopleura* but this female had probably been fertilized by a hybrid male or even by both *melanopleura* and *annectans* males before it was captured.

The *humeralis* beetles reared from the first pair mentioned were used for breeding purposes and all the individuals reared came true to type, about thirty beetles maturing.

It was now indirectly evident that mixing was quite common between *melanopleura* and *annectans* and that it sometimes occurred between *annectans* and *humeralis*, but there was no evidence that it occurred between *melanopleura* and *humeralis*. To ascertain whether this latter were possible and also to make the actual crosses in the other cases in order to further investigate the law of heredity, efforts were made to cross *humeralis* as often as possible with *annectans* and *melanopleura*. *Humeralis* was found to hybridize just as freely with one form as with the other. No more difficulty was encountered than would be expected even among members of the same form under the same circumstances. On one occasion an *annectans* male chose a *humeralis* female even though a female of its own kind was present in the cage.

Unfortunately only one female of *humeralis* was available for this purpose sufficiently early in the season, but there were several males which proved capable and these were crossed with females of both *melanopleura* and *annectans*. The female of *humeralis* that was used was probably the one that produced all of the above mentioned 30 *humeralis*, all true to type, she, at any rate produced a large proportion of them. This beetle was crossed with an *annectans* male but she died so soon that only two beetles were reared from this union. They were *annectans* but were too feeble for further breeding. An *annectans-humeralis* hybrid female was mated with a *melanopleura* male and later with an *annectans* male. This female had previously been kept in a cage with its brothers and the eggs laid had produced seven *humeralis* and four *annectans*, but after these crossings no more *humeralis* appeared though forty-seven beetles were reared. Three crosses were made by means of the *humeralis* males and *melanopleura* and *annectans*

females and from these 169 beetles were reared in the first generation. All but one were either *melanopleura* or *annectans* according to the composition of the female. This one exception was a *humeralis* beetle. A noticeable character of the progeny of these crosses was the greater vigor of the individuals so that a larger percent matured as compared with the purer strains. From one of the above three pairs, an *annectans* female and a *humeralis* male, the first generation of which consisted of fifty-seven *annectans*, four second generation beetles were reared and they proved to be two *annectans* and two *humeralis*. The beetles then refused to lay any more eggs and seemed to be preparing for hibernation. They had been unavoidably subjected for a few days to a temperature low enough to stiffen them up considerably and cause them to nearly cease eating and the subsequent removal of them to an almost summer temperature, though it caused the eggs to hatch in half the time they had under the low temperature and increased the appetites and rate of growth of the larvae quite remarkably, failed to cause the beetles to lay any more eggs. Work had, therefore, to close for the season at this interesting point, and the beetles were put into hibernation.*

From these crosses there is another lesson to be learned besides the relation of *annectans* and *melanopleura* to *humeralis*, namely; something about the heredity between *melanopleura* and *annectans* themselves. The process of mating these forms with *humeralis* which is recessive to both, served as a test of the germinal composition of the member of the pair carrying the dominant characters. In the case where two *melanopleura* females, which had been isolated from *annectans* from time of emerging were crossed with *humeralis males* there were produced 29 *melanopleura* to 25 *annectans*, and 31 *melanopleura* to 26 *annectans* respectively. *Melanopleura* was in each case a little in excess of 50 percent. In the case of the *annectans-humeralis* hybrid female mated with the *melanopleura-annectans* male the progeny was 19 *melanopleura* and 28 *annectans*. The higher percent of *annectans* was doubtless due to the fact that an *annectans* male was put into the cage during the latter

* Just as this article was ready to send to the publisher a lot of second generation beetles, from the *melanopleura* females crossed with the *humeralis* males, emerged. From the eggs of the first generation *melanopleura-humeralis* hybrids there were reared 19 *melanopleura* and 7 *humeralis*. From the eggs of the first generation *annectans-humeralis* hybrids there matured 12 *annectans* and 5 *humeralis*. These figures come very near to the Mendelian ratio for progeny of hybrids.

part of the period, because just before the last three batches the proportion was 16 *melanopleura* and 18 *annectans*, and the last three batches gave 3 *melanopleura* and 10 *annectans*, thus making a sudden change in the proportion. This male was in all probability pure *annectans* as there has not been found, in my experience, any proven case of *annectans* carrying *melanopleura* characters. The characters carried by the female could have had no influence whatever in the results, since neither of the characters carried by the female was dominant to the characters carried by the male. Either the *melanopleura* or the *annectans* characters of the male would realize themselves whether they met an *annectans* or a *humeralis* character of the female. These results approximately show that the *melanopleura-annectans* hybrids carry the characters in the proportion of half and half. The somewhat high percentage of *melanopleura* obtained in these cases was more than balanced by the extremely low percentage obtained in the case of the progeny of the cage of *melanopleura-annectans* hybrids, in which case *melanopleura* constituted less than half of the progeny when it should have constituted three-fourths. The mortality in this latter case, however, was so great that the data are hardly sufficient.

Another *melanopleura* female from *melanopleura-annectans* hybrid parents after being fertilized by some of its *melanopleura* brothers was isolated for a few days, during which time it laid three batches of eggs. From these eggs were reared 9 *melanopleura*, 3 *humeralis*, and 1 *annectans*. Excepting the one *annectans*, this was just the right proportion for the progeny of two hybrids according to the Mendelian law. This *annectans* individual, (if it did not get in by mistake which was very unlikely, great care having been exercised) must have been due to fertilization by a *melanopleura-annectans* male probably before the *melanopleura-humeralis* male. The female was then mated with a *humeralis* male and after that 14 adults were obtained, 6 *melanopleura* and 8 *annectans*. The results in this case seem to indicate that there had been a cross between the *melanopleura* ancestors of this female and *humeralis*, while still in nature and that in the first generation reared in captivity the dominant *melanopleura* had kept it concealed, so that it was not until the second generation that the crossing between two hybrids happened to take place, thus allowing the *humeralis* character to appear.

From the cross between an *annectans* female (reared from *melanopleura* parents) and a *humeralis* male 57 beetles matured all *annectans*. This showed the female to be pure strain though descended from *melanopleura* parents.

The foregoing results are given below in tabulated form:

	mel.	col.	ann.	hum.	total
Crosses					
1 Male—*annectans* / Female—*humeralis* } 1st gen.			2		2
2 Male—*humeralis* } 1st gen.			57		57
Female—*annectans* } 2nd gen.			2	2	4
3 Male—*humeralis* } 1st gen.	29		25		54
Female—*melanopleura** } 1st gen. (2d gen.)	19			7	26
4 Male—*humeralis* } 1st gen.			12	5	17
Female—*melanopleura** } 1st gen.	31		26	1	58
5 Male—*melanopleura** and later *annectans* } 1st gen.	16		18		
Female—*annectans-humeralis* hybrid } 1st gen.	3		10		47
Humeralis Hybrid					
Female—*annectans-humeralis* / Male—*annectans-humeralis* } offspring			7	10	17
Female—*melanopleura-humeralis* / Male—*melanopleura-humeralis* (probably). Also *melanopleura-annectans* (prob.) }	9		1	3	13
Female—*melanopleura-humeralis* / Male—*humeralis* } offspring.	6			8	14
Melanopleura-annectans Hybrids					
Cage of males and females—offspring	11	3	16		30
Female captured, male *annectans?* —offspring	7		6		13
Two females and one male mated with recessive—offspring (See crosses 3, 4 and 5)	76		69	1	
	94	3	91	1	
Annectans					
Cage of males and females—offspring			19		19
One female, captured, male unknown, offspring			6		6
One female with *humeralis* male (See cross 2)—offspring			57		
			82		
Humeralis					
One female with 3 males—offspring (Female used later in cross 1)				30	30
Total					407

* melanopleura-annectans hybrid.

From the foregoing results the following conclusions seem to be quite evident:

I. *Melanopleura* is dominant over *annectans*, *coloradensis*, and *humeralis*, and the heredity is segregate.

1. Over *annectans* since

a. The hybrid form between *melanopleura* and *annectans* is *melanopleura*. Of the progeny, 30 in number, of a cage of *melanopleura*, *annectans* constituted over half. In the progeny of two females and one male tested by mating with *humeralis* there appeared 76 *annectans* and 69 *melanopleura*, altogether, which is very close to the Mendelian ratio for the segregation of characters in hybrids.

b. *Annectans* has in no case given evidence of carrying *melanopleura* characters. The 25 progeny from a cage of *annectans* showed no *melanopleura* characters nor did any of the 57 progeny of the *annectans* female mated with *humeralis*.

2. Over *coloradensis* since the hybrid form between *melanopleura* and *coloradensis* is *melanopleura* as is shown by the fact that 3 *coloradensis* appeared among the offspring of *melanopleura* parents.

3. Over *humeralis* since

a. The hybrid form between *melanopleura* and *humeralis* is *melanopleura*. In the first generation from three crosses of *melanopleura* with *humeralis* or with *annectans-humeralis* hybrids, *humeralis* appeared but once among 159 individuals. A *melanopleura-humeralis* female mated with its brothers gave 9 *melanopleura*, 1 *annectans*, and 3 *humeralis*. The same female mated with a *humeralis* male gave 6 *melanopleura* and 8 *humeralis*, approximately showing the segregation of characters to be according to the Mendelian law. The second generation from crossings of *melanopleura* with *humeralis* consisted of 19 *melanopleura* and 7 *humeralis*.

b. *Humeralis* has given no evidence of carrying *melanopleura* characters. The 30 offspring from *humeralis* parents all came true to type.

II. *Annectans* is dominant over *humeralis* since

a. The hybrid form between *annectans* and *humeralis* is *annectans*. In the cross between *annectans* and *humeralis* *humeralis* did not appear at all in the first generation of 57 progeny, but did appear in half of the second generation which consisted of 4 beetles. *Annectans-humeralis* hybrids mated with each other produced 7 *annectans* and 10 *humeralis* in one case, and in another 12 *annectans* and 5 *humeralis*.

b. *Humeralis* has given no evidence of carrying *annectans* characters, as shown by the 30 offspring of *humeralis* parents all true to type.

This subject is still unfinished and experiments are now in progress to determine the relation of *coloradensis* and the rather albinic form of *annectans* to the other forms.

It would be interesting to interbreed these forms with other species of *Adalia*, especially with the European *frigida* Schneider and with *bipunctata* Linneaus.

Observations were also made on the beetles used in the foregoing experiments for the purpose of ascertaining the heritability of the characters of the spots on the elytra in *annectans* and of the markings of the pronotum in this same form and in *melanopleura*. The progeny resulting from the mating of *annectans* and *melanopleura* beetles with the recessive *humeralis* were examined when the number was large enough to afford sufficient data. The beetles in these cases were particularly advantageous for this purpose because the dominant characters would be the only ones to show in the first generation, thus reducing the number of strains which would appear to one or two. In the case of the *melanopleura-annectans* hybrids there would be one strain of *annectans* and one of *melanopleura*, which would afford a very simple series and show very plainly whether these characters behave at all as unit characters or whether they seem to be fluctuating variations. The results are shown in the drawings Figures 2 to 7, Plates XX to XXII.

In the markings of the pronotum, special attention was paid to the character of the lateral black spot and the extent to which was it enclosed by the surrounding white. The median posteriorly pointed dash of white from the apical margin and also the basal marking of whitish are sometimes very small or even absent; but in this study only secondary attention was paid to these and the drawings, except curve (e), Fig. 7, Plate XXII, are arranged in series according to the aforesaid black spot. The pronota of *melanopleura* and *annectans* are arranged separately in each case.

In the case of the elytra primary attention was paid to the confluence of the spots, and the series is arranged according to the number of confluences in each case. The parents of each series are drawn in full or designated above and the first generation progeny in a row below. The numerals below each drawing indicate the number of individuals in that class. As the *humeralis* parent seems to have no influence on the char-

acters of the first generation it was not thought necessary to draw this parent.

Figure 2, Plate XX represents the *annectans-humeralis* hybrid female and her progeny resulting from union with a *melanopleura-annectans* hybrid male, and also for the last few days of the experiment, with a pure *annectans* male. The numbering of the spots is after Weise taken from Johnson 1910. In this case the progeny would contain four strains of *annectans*, one from the mother, one from the *melanopleura-annectans* father, and two strains from the *annectans* father, which, however, could hardly have affected more than the last three batches of eggs. This would be just the number of strains to be represented if two members of *annectans* were mated. The males in this case were both lost and so can not be shown in the figure. Of the batches after the *annectans* male was introduced, in the elytra series, one beetle was in class (d), six in class (e), three in class (f), and one in class (i). In the pronota series four were in class (k) and seven in class (l). There was considerably less variation among these than in the foregoing batches, but whether it was due to the *annectans* male or to environmental influences can not be ascertained with certainty; but as these were reared later in the season than the foregoing batches, during the latter part of August and the early part of September, during which time an unusually cold wave occurred, the only environmental influence would probably have been a lower temperature. This factor, however, would, from the experience of Tower* and Johnson, be expected to produce a melanic effect, but here the difference was albinic rather than melanic, so the case does not seem to be explained by the environmental factor, and unless it was produced by some unknown cause, seems most probably to have been due to heredity factors introduced by the *annectans* male.

It will be noted in this case, Figure 6, curve (a), Plate XXI, and Figure 7, curves (a), and (b) Plate XXII, that all of the beetles, of both *melanopleura* and *annectans*, which were reared from this female were rather at the albinic end of the scale as to both elytral and pronotal characters. In the elytra none have more than two full confluences and the mother ranks at

* Tower, William Lawrence, 1906. An Investigation of Evolution in Chrysomelid Beetles of the Genus Leptinotarsa. Carnegie Institution of Washington, Pub. No. 48.

about the middle of the series and at one of the highest points of the curve. In the case of the pronotum the mother was decidedly more melanic than the apex of the curve for either *annectans* or *melanopleura*. The curves for these two forms were not alike, annectans having the greatest number, 45 per cent at the albinic end of the scale with the black spot well enclosed by the surrounding white. In the *melanopleura* series only 11 per cent were at this point, the largest number, 83 per cent, having the black spot rather weakly enclosed. None of the *annectans* here showed the red pattern on the elytra, as shown in Figure B, Plate XIX, though the mother shows it faintly.

Figure 3, Plate XX, represents the *annectans* female crossed with *humeralis* male. In this case we would expect to find only two strains of *annectans*. Here, however, the variation was considerably broader than in the former case where four strains were represented, the curve beginning at the same point of albinism as the former case and extending to four and a half confluences (that is to four and a pronounced tendency to a fifth confluence), Figure 6, curve (b). The mother was several degrees more albinic than the highest point of the curve. Note here that in the mother there is an absence of spot 4 and also that there is a small spot between spots 1 and 2, which, though very unusual, probably denotes tendency to confluence between spots 1 and 2. Neither the presence of this extra spot nor the absence of spot 4 show in any of the progeny examined, though both confluence and tendency to confluence appear between spots 1 and 2. The mother of these seems to have shown nothing of the red pattern mentioned above and shown in Figure B, Plate XIX, but in the 37 offspring, 9 showed it very plainly, 16 moderately plain, 4 faintly, and in 6 it was absent.

Figure 4, Plate XXI shows a *melanopleura-annectans* hybrid female, crossed with a *humeralis* male, and her first generation progeny. Here there can be but one strain of *annectans* to appear in the progeny. The curve of variation, Figure 6, curve (c), Plate XXI, covers a somewhat wider range of variation than in the case of the first instance, curve (a) where four strains are represented, the largest number of confluences being three. Here 23 out of 27 or 85 percent lack spot 6. In the pronota of *annectans* a peculiarity was observed in that sometimes either the basal marking or the apical median dash were lacking.

For these pronota two curves were given, Figure 7, curves (d) and (e), curve (d) to show the variation of the lateral spot only and (e) to represent the general melanism when the other markings are considered, each degree representing about the equivalent of the melanism of the state of the lateral spot as given in the legend for the respective columns. The curve for *annectans* in this series was much broader than that for *melanopleura*. The mother was rather toward the albinic end of the series for *annectans* and at the melanic end for *melanopleura*. All of the *annectans*, 27 in number, had the red spots on the elytra, as shown in Fig. B, Plate XIX.

Figure 5, Plate III, shows another *melanopleura-annectans* hybrid, female mated with a *humeralis* male, and her first generation progeny. Here again would be but one strain of *annectans*. The range of variation in the elytra of *annectans* was not very broad, showing none of the more albinic forms, the curve, Figure 6, curve (d), Plate XXI, beginning at one confluence and extending to three and a half confluences. In the pronota of the *annectans* series, Figure 7, curve (g), Plate XXII, uniformity almost obtains, 93 per cent having the lateral spot well enclosed and 7 per cent being one-fifth enclosed. In the *melanopleura* series, however, the curve, Figure 7, curve (h), Plate XXII, is very broad extending to a degree of melanism that is quite rare. The mother ranks at the albinic end of the scale though the highest part of the curve for her *melanopleura* offspring is four degrees further to the melanic end of the scale.

GENERAL OBSERVATIONS.

In comparing the curves for the elytra it must be born in mind that the chief points of comparison are the melanic positions of the range and highest points of the curves. Since the number of individuals represented by each of the curves was not uniform, the exact number on any one line shown by the different curves is not truly comparable; only the melanic position of high and low points and range in each curve can be compared with the same in another curve.

It will be noted that each curve has one or two points that are much higher than any other points in the curve, and that these high points in the different curves vary greatly in melanic position, also that the curves vary considerably in their range. It seems as though these high points in the curves might represent centers of variation. The curves would then signify that different strains of these beetles have different centers of

variation and different scopes of variation. Curve (c), Figure 6, Plate XXI, which represents but one strain of *annectans* covers a wider range than curve (a) which represents four strains. Curve (d), which also represents one strain is quite narrow, seeming to signify that this strain had a greater degree of constancy than the others. The mother in each of these cases occurred within the range of variation for her progeny but not always at the highest point of the curve though in both of the instances where this observation was possible she occurred at one of the high points, see curves (a) and (b), Fig. 6, Plate XXI. Two of the mothers being *melanopleura* had no place in the elytra series, and since in the cases where the mother was *annectans* two or more strains were represented, the fact of the highest part of the curve not being at the same position as the mother might in this case be explained as due to one of the other strains involved.

There seemed in some cases to be a certain measure of heritability of different characters in the color pattern of the elytra. The absence of spot 6 in Figure 4, Plate XXI, seemed to be inherited to a large degree since it was lacking in 21 out of 27 beetles. The mother being *melanopleura* could not be observed on this point. This spot seems from my observations to be the one most frequently lacking in this form, indeed almost the only one except in a small minority of beetles. Spot 4 was absent in only three beetles in this study, in Figure 3 (a), Plate XX, and in two others not drawn but ranked with (f) and (g) respectively in Figure 2, Plate XX, spot 5 was faint in one, Figure 3 (c). The absence of spot 4 seemed not to be inherited in these cases, as no case of absence occurred in the 37 progeny of the mother, Figure 3 (a), which lacked it, and it appeared only twice in the 30 offspring in Figure 2, Plate XX.

Some observations were made on the order in which confluences take place. Spots 6 and 7 seemed to be the first as a rule to connect, as in this study there was only one instance where a beetle showed confluences and had these spots separate, see Figure 3 (e). There were three such cases where spot 6 was absent, but even in the case of absence there was often a projection toward its position from spot 7 as though in these instances the confluence was even more persistent than the spot itself. After this confluence no further order was observed except that between spots 4 and 5 it seemed to be the most unusual and perhaps the last in order.

In the case of the pattern of reddish spots on the elytra of *annectans* Figure B, Plate XIX, it seemed as though there might be segregation in some cases at least, and that the absence of the character was dominant to its presence. In the series in Figure 2, Plate XX, it shows faintly in the mother (the dimness may be due to fading after death as this character was not recorded during life) and it was plainly evident in the mother and a brother of this beetle, in fact in all of the individuals of this strain that have been preserved. It shows in none of the 30 progeny of this beetle, but this absence may be explained as due to the males, which being lost, can not be examined as to their possession of the character.

In the series in Figure 3 where the mother does not show the marking but carries two strains of *annectans*, it appeared in five-sixths of the beetles to a greater or less degree. As the male in this case was *humeralis* both of these strains must have come from the mother and its absence in her development would seem to signify the dominance of the absence of the character over its presence. The proportion, however, found in the progeny seems rather puzzling unless the *humeralis* character from the male could have had any influence in the proportion, which seems unlikely.

In the series in Figure 4, Plate XXI, it appeared in all of the 27 *annectans* progeny. The mother, being *melanopleura* of course does not show it. In the series in Figure 5, Plate XXI, some show it and some do not. The exact number in each case can not be determined as some of the beetles have developed so much of the red color in their elytra during hibernation that it is impossible to tell with certainty whether they possess the character or not. The mother being *melanopleura* of course does not show the character. The fact that some clearly show its presence and others just as clearly show its absence when they are all from one strain of *annectans* seems to be evidence against segregation in this case.

In the pronota curves in Figure 7, Plate XXII, the matter is a little more complex as there are both *annectans* and *melanopleura* to be represented for each female except one, Figure 2, Plate XX. As the curves for these two forms even when from the same parents were different in every case not only in the position of the apex but also in range and sometimes very different, it would seem that each strain keeps distinct; that is, the pronotal characters of *annectans* do not mix with those of *melanopleura*.

When, however, the characters of the mother are compared with those of her offspring which are of the same form as herself little uniformity was found. In no case did she rank at the highest point of the curve, neither did she ever occur at the lowest point, nor ever outside of the range of variation for the offspring. There seemed to be some degree of heredity but it was not constant. The results appear a good deal the same as in the elytra, that there are centers of variation and a certain limit of range that were inherited to a greater or less degree, but with no evidence of segregation of unit characters such as occurs between *melanopleura*, *annectans*, and *humeralis*.

ADDENDA.

Since sending the foregoing article to the publisher results have been obtained in the experiments concerning the relation of *coloradensis*, the so-called albinic form of *annectans*, and a similar form of *melanopleura* to the other forms treated. The albinic form of *annectans*, so-called for want of a better name is above described separately under *annectans* and figured at F, Plate I. The albinic form of *melanopleura* is identical with that of *annectans* in pronotal characters, namely, it lacks the lateral dot, the lateral margin of the pronotum being broadly pale as in *coloradensis;* in all other characters it agrees with *melanopleura*. The results obtained are tabulated as follows:

Parents				1st gen. Offspring						total
Male		Female								
Appearance	Characters carried†	Appearance	Characters carried†	M	al. M	al. A	A	C	H	
C	C and H	H	H					4	3	7
unknown	M and A	al. A	C and A	4	2	1	1			8
H	H						3	2		5
H	H	al. M	C and M	3				1		4
C	C and H	M	M and H	6	7			4	6	23
al. A.	C and A	M	M and H	3	3		3	2		11
al. A.	C and A	al. A.	C and A			13	5	5		23
‡A	A and H	H	H				7		10	17
		A	A and H				11		2	13
al. M.....	C and M	al. M.	C and M		4					4
			Total..	16	16	14	30	18	21	115

*A means *annectans;* C, *coloradensis;* H, *humeralis;* al. A. albinic *annectans;* al. M, albinic *melanopleura*.

†These are given as shown by the offspring when not known from pedigree breeding.

‡This male was, judging from appearance, an intergrade between *annectans* and albinic *annectans*. It lacked the basal spots on the elytra but possessed the lateral dot on the pronotum, which latter seems to be the ultimate distinguishing character.

These results seem to furnish conclusive evidence

1. That *coloradensis* is a good variety or type equal with *melanopleura*, *annectans*, and *humeralis*, acting as a unit character in heredity.
2. That when crossed with *annectans*, *coloradensis* produces a blended hybrid, in both elytral and pronotal characters, namely the form above referred to as an albinic form of *annectans*.
3. That when crossed with *melanopleura* a blend is produced in the pronotal characters, identical with the *annectans* blend; but in the elytra *melanopleura* dominates entirely.* This form was mentioned in the description of *melanopleura* as a "more albinic form."
4. That when crossed with *humeralis coloradensis* dominates perfectly so that the hybrid form is indistinguishable from the pure strain of *coloradensis*.

It seems that in every instance the more albinic character dominated over the more melanic one; for example: immaculate elytra, in *melanopleura*, dominate over the spotted ones of each of the other forms. The absence of the black lateral dot in the pronotum, in *coloradensis*, dominates over its presence in each of the other forms. The presence of the whitish basal marking on the pronotum, of *annectans* and *melanopleura*, dominates over its absence in *coloradensis* and *humeralis*. The absence of the basal elytral spots, in *coloradensis*, dominates over its presence in *annectans*. The usual absence of confluence in the median and apical series of spots in *annectans* dominates over the confluence in these spots in *coloradensis*. *Humeralis* which presents the most melanic characters in every particular in both elytra and pronotum is perfectly recessive to each of the other forms.

The inheritance of the faint lateral dot on the elytra in *melanopleura* was observed in the specimens at hand but no law was ascertained. It seems to be a mere fluctuating variation.

The single *humeralis* beetle mentioned in the article as appearing among the first generation offspring in the 4th cross in the table, between *humeralis* and *melanopleura* parents, was tested in breeding. It proved to be a male and was put into a cage with two *humeralis* females, from the eggs of which seven progeny were reared to maturity. All of these were *humeralis*

* This statement is to be reconciled with the statement in the foregoing article that *melanopleura* is dominant over *coloradensis* by the fact that at that time the hybrid was considered as only a variant of *melanopleura*.

which seems to prove that the beetle in question was pure strain. This beetle may possibly have gotten into the cage by mistake in spite of the great care exercised as several dozen cages containing larvae of all the forms were being tended and cleaned daily.

Five other offspring were reared from *humeralis* beetles obtained in these experiments, and these all came true, making 42 progeny in all reared from *humeralis* parents, breeding true in every instance.

Two *humeralis* beetles without dorsal spots were obtained as the progeny resulting from a cross between a *melanopleura* male, (evidently a *humeralis* hybrid) from out of doors, with an *annectans-humeralis* female representing the third generation of *humeralis* reared in the laboratory. All of the ancestors and progeny, two in number, of this female, by a former mating showed the dorsal spots normally developed. These two beetles were the only progeny obtained from this union and efforts to rear offspring from them, though they proved to be male and female, have thus far been fruitless, seemingly due to a weak constitution as the eggs hatch poorly. The male seemed weak and both beetles died soon. It would seem from this case that the absence of these spots dominated over its presence, which is contrary to the behavior of heredity with regard to the other characters of this group. If this is not the case the strain in the laboratory must have carried this character of absence through three generations without it having a chance to meet its equal so as to be able to realize itself.

Another cross which was made between an *annectans* male and a *humeralis* female last August but which laid no eggs until this, the following spring, produced in the first geneartion 26 beetles, all *annectans*. The *humeralis* female was later used in the first cross represented in the first table in addenda.

EXPLANATION OF PLATES.

PLATE XIX.

FIG. A. *Adalia melanopleura* Leconte.
FIG. B. *Adalia annectans* Crotch.
FIG. C. *Adalia annectans* Crotch.
FIG. D. *Adalia humeralis* Say.
FIG. E. *Adalia coloradensis* Casey.
FIG. F. *Adalia annectans* Crotch.
FIG. G. *Adalia melanopleura* (more albinic form).
FIG. H. Pupa of *A. annectans, melanopleura, coloradensis,* and *humeralis.*
FIG. I. Larva of *A. annectans, melanopleura, coloradensis and humeralis.*
FIG. J. Eggs of *A. annectans, melanopleura, coloradensis and humeralis.*
All drawings are magnified 5 diameters.

PLATE XX.

FIG. 1 shows in diagram the results of the foregoing experiments in inheritance between *annectans, melanopleura, coloradensis, and humeralis.* The numerals beneath the circles in each case indicate the number of individuals in that class. The lines connecting with higher circles indicate parentage in each case.

FIG. 2. *a* and b—characters of *annectans-humeralis* female, mated with males indicated.
c to *j*—elytral characters of *annectans* offspring.
k to *n*—pronotal characters of *melanopleura* and *annectans* offspring.
Numerals indicate number of individuals in the class in each case.

FIG. 3. *a*—elytral characters of *annectans* mother, mated with male indicated.
b to *o*—elytral characters of *annectans* offspring.
p to *v*—pronotal characters of *annectans* offspring.
Numerals indicate number of individuals in each class.

PLATE XXI.

FIG. 4. *a* and *b*—characters of *melanopleura annectans* mother mated with male indicated.
c to l—elytral characters of *annectans* offspring.
m to *t*—protonal characters of *annectans* offspring.
u to *v*—pronotal characters of *melanopleura* offspring.
Numerals indicate number of individuals in each class.

FIG. 5. *a* and *b*—characters of *melanopleura-annectans* mother, mated with male indicated.
c to *d*—pronotal characters of *annectans* offspring.
e to *k*—elytral characters of *annectans* offspring.
l to *r*—pronotal characters of *melanopleura* offspring.
Numerals indicate number of individuals in each class.

FIG. 6. Shows the curves representing the variation in the elytral characters of the *annectans* offspring, drawn in the foregoing figures. The numerals on the left show the number of individuals. The degrees of melanism are designated by the legend below in each case, the most albinic being at the extreme left and the most melanic at the right. "Confluence ½"means one case of tendency to confluence, "confluence ¾" means two cases of tendency to confluence. The latter is here given a rank of its own as it does not seem equal in melanism to one full confluence. The curve above the legend "spot 6 absent" does not represent all the individuals lacking that spot, but only those with no case of confluence.

Curve (a) represents the series in Fig. 2, Plate II. The full line triangle shows the position of the mother in this series.

Curve (b) represents the series in Fig. 3, Plate II. The broken line triangle represents the position of the mother.

Curve (c) represents the series shown in Fig. 4, Plate III.

Curve (d) represents the series shown in Fig. 5, Plate III.

The mother of the series for curves (c) and (d) were *melanopleura* and so have no place in this diagram.

PLATE XXII.

FIG. 7 shows the curves for the pronotal series.

Curve (a) represents pronotal characters of *annectans* offspring shown in Fig. 2, Plate II.

Curve (b) represents pronotal characters of *melanopleura* offspring in Fig. 2, Plate II.

The open triangle represents the mother of the series represented by curves (a) and (b), Fig. 2, *a* and *b*, Plate II.

Curve c) represents the *annectans* series in Fig. 3, Plate II.

Curve (d) represents the *annectans series* in Fig. 4, Plate III.

Curve (e) represents the *annectans* series in Fig. 4, Plate III, according to general melanism.

Curve (f) represents the *melanopleura* series in Fig. 4, Plate III.

The open triangle represents the mother, Fig. 4, *a* and *b*, Plate III.

Curve (g) represents the *annectans* series, Fig. 5, Plate III.

Curve (h) represents the *melanopleura* series, Fig. 5, Plate III.

The solid triangle represents the mother Fig. 5 (a) and (b), Plate III.